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RESEARCH ARTICLE

Overwintering strategy regulates phenological sensitivity and consequences for ecological services in a clade of temperate North American insects

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Abstract

1. Recent reports of insect declines have raised concerns about the potential for concomitant losses to ecosystem processes. However, understanding the causes and consequences of insect declines is challenging, especially given the data deficiencies for most species. Needed are approaches that can help quantify the magnitude and potential causes of declines at levels above species.
2. Here we present an analytical framework for assessing broad-scale plant–insect phenologies and their relationship to community-level insect abundance patterns. We intentionally apply a species-neutral approach to analyse trends in phenology and abundance at the macroecological scale. Because both phenology and abundance are critical to ecosystem processes, we estimate aggregate metrics using the overwintering (diapause) stage, a key species trait regulating phenology and environmental sensitivities. This approach can be used across broad spatiotemporal scales and multiple taxa, including less well-studied groups.
3. Using community ('citizen') science butterfly observations from multiple platforms across the Eastern USA, we show that the relationships between environmental drivers, phenology and abundance depend on the diapause stage. In particular, egg-diapausing butterflies show marked changes in adult-onset phenology in relation to plant phenology and are rapidly declining in abundance over a 20-year span across the study region. Our results also demonstrate the negative consequences of warmer winters for the abundance of egg-diapausing butterflies, irrespective of plant phenology.
4. In sum, the diapause stage strongly shapes both phenological sensitivities and developmental requirements across seasons, providing a basis for predicting the impacts of environmental change across trophic levels. Utilizing a framework that ties thermal performance across life stages in relation to climate and lower-trophic-level phenology provides a critical step towards predicting changes in ecosystem processes provided by butterflies and other herbivorous insects into the future.

KEYWORDS
abundance, diapause stage, ecosystem processes, insect decline, Lepidoptera, nutrient cycling, phenological mismatch, phenology

1 | INTRODUCTION

Herbivorous insects are crucial components of forest ecosystems, sitting in the middle of dense food webs, where they interact with lower trophic levels as primary consumers and higher trophic levels as key food resources. However, our understanding of insect contributions to ecosystem processes, especially impacts on higher and lower trophic levels, is based on limited empirical evidence (Noriega et al., 2018). Because insects exhibit a diverse range of complex, multi-stage life histories and are enormously diverse, simply properly identifying species is challenging and is limited by available taxonomic knowledge. Quantifying contributions to ecosystem function, or proxies such as community abundance, is hindered by challenges to monitoring herbivorous insects across their immense functional and taxonomic diversity, which limit the availability of broad-scale data (Cardoso et al., 2011). These knowledge gaps are pressing given the dramatic insect population declines reported recently (Hallmann et al., 2017, 2020; Warren et al., 2021), and the potential consequences of those declines across ecosystems (Wagner, 2020). Scientists have raced to assemble long-term monitoring records in order to document the tempo and mode of these declines across different ecoregions (e.g. EntoGEM, InsectChange; Grames et al., 2019; van Klink et al., 2021) and to sound an alarm for society as a whole (e.g. Cardoso et al., 2020; Harvey et al., 2023). However, still needed is a scalable framework for understanding the interactions of intrinsic drivers, for example key life history traits, and extrinsic factors, such as the availability of food resources, that provide a more explanatory basis for understanding this developing crisis and its impact across ecosystems.

At the macroecological scale, ecosystem processes provided by a given group may often be reasonably proxied by abundance dynamics (Wagner, 2020; Winfree et al., 2015). For insects, population trajectories are dramatically shaped by climatic changes (Halsch et al., 2021; Harvey et al., 2023). Climate drivers may be both direct, for example through temperature's impact on insect developmental rates, reproduction and mortality (Buckley et al., 2017), or indirect, such as changes in survival due to a declining abundance of food sources and trophic mismatch. Trophic mismatches occur when climatic changes differentially affect the relative abundance and phenology of communities that exist at lower (food resources) and higher (predators and natural enemies) trophic levels (Miller-Rushing et al., 2010). Seasonal trophic mismatches caused by differential phenological sensitivities to climate may be particularly influential for yearly insect abundances and longer-term population dynamics, though not all studies have detected clear relationships between cross-trophic phenology shifts and abundance change (Abarca & Lill, 2015; Kharouba et al., 2015; Schwartzberg et al., 2014; Singer & Parmesan, 2010; Stewart et al., 2020; Visser & Gienapp, 2019). In general, while climate-driven phenological shifts tend to be relatively consistent across clades and geography, species abundance patterns are often more variable (Høye et al., 2021). Nevertheless, declines in one trophic level will ripple up the food chain regardless and may or may not be exacerbated by additional trophic mismatches.

The ecosystem processes provided by herbaceous insect populations are intimately connected to their life stage, phenology and abundance. Contributions to ecosystem function provided by a species in the larval stage, often as consumer or prey, are different from those provided in the adult stage. Environmental sensitivities also differ by life stage (McDermott Long et al., 2017). Key species' life history traits are also critical for determining the relationship between phenology and abundance within and across trophic levels (Hällfors et al., 2021; Ju et al., 2017; Michielini et al., 2021). For insects, traits that impact ecophysiological responses to temperature cues across life stages are particularly important (Breed et al., 2013; Diamond et al., 2011; Eskildsen et al., 2015; Macgregor et al., 2019; Zografou et al., 2021). For temperate insects, many species rely on diapause to survive harsh winter conditions. Diapause strategies vary across species between egg, larval, pupal and adult overwinterers, and these states determine thermoregulatory ranges and sensitivity (Abarca et al., 2024; Kingsolver & Buckley, 2020). Because temperature is a direct driver of insect developmental rates, species overwintering in earlier developmental stages are likely to experience greater climate-driven phenology shifts in seasonal adult emergence (as opposed to peak or median flight phenology, per Kharouba et al., 2014). Further, late-instar larvae or pupae enter the growing season with greater energy reserves and fewer developmental requirements than eggs or early-instar larvae, which may bolster resilience to changing stressors. Indeed, Breed et al. (2013) found that butterflies overwintering as eggs have been more likely to be locally declining in Massachusetts. Thus, both physiological knowledge and field studies suggest that the diapause stage may be of particular importance in determining variability and trends in phenology and abundance (Breed et al., 2013; Diamond et al., 2011, 2014; Karlsson, 2014).

Delineating a stronger trait-based (as opposed to species-based) and multi-trophic approach to understanding insect population trends is especially needed considering reported declines and current projections for environmental change. To address this need, we leverage different community science data resources that inform about phenology (e.g. eButterfly and iNaturalist; Di Cecco et al., 2021; Prudic et al., 2017; Unger et al., 2020) and abundance (North American Butterfly Association counts; Taron & Ries, 2015) at broad spatial extents. This approach allows direct testing of critical but as yet unanswered questions about how life history traits and phenological shifts impact abundance trends in insects. By focusing on one critical life history trait, rather than

species identities, this framework can be applied to test predictions for phenology and abundance dynamics in other holometabolous insects (comprising the majority of described species; Costello et al., 2012; Groombridge & Jenkins, 2002). Given the lack of sufficient data for large-scale studies of most insect species, trait-based approaches can provide needed insights for these diverse taxa, even for groups that are poorly studied. While individuals (within and among species) differ in their contributions to ecosystem function, the overall similarities among taxa sharing certain life history traits and/or phylogenetic histories allow for aggregate metrics to approximate the ecosystem processes provided by many species.

Here, we assess the potential for trophic mismatch by comparing phenology shifts across trophic levels for insects according to the overwintering diapause strategy. We then link these results, along with climatic drivers, to the demographic performance for butterflies in the Eastern USA. We developed our predictions based solely on abundances summed by the overwintering stage without regard to species identity, to focus broadly on changes related to ecosystem function and to test the potential of this approach for less well-studied insects. We make the following key predictions:

1. Broad-scale plant leaf-out and insect emergence phenologies show different sensitivities to both winter and spring climate drivers, leading to potential trophic mismatches.
2. Phenological sensitivity to climate is strongly determined by the life stage of insect winter diapause, and insects that overwinter in earlier life stages will show greater shifts in adult emergence phenology under warmer winter and spring conditions.
3. Abundance declines are strongest for insects overwintering in earlier life stages due to higher sensitivity to climatic and plant phenology shifts.

2 | MATERIALS AND METHODS

2.1 | Study domain

We examined broad-scale patterns in aggregated phenology and abundance of adult insects (butterflies, Superfamily Papilionoidea) for 2001–2017 in eastern North America, using a study area bounded by (32° N, 50° N) and (95° W, 60° W), a region with distinct winters each year. In order to determine broad-scale phenology patterns amenable to integrating results across trophic levels, data were aggregated within a uniform hexagonal grid (Icosahedral Snyder Equal Area projection with an aperture of 3; distance between cell centres of 285 km; per cell area of ~70,000 km^2, Figure 1a,b) that has previously been used in avian phenology studies (Youngflesh et al., 2021) and thus provides a basis for further extending broad-scale studies across multiple trophic levels. We focused on resident insects, which survive winter by entering a period of diapause at species-specific developmental stages (egg, larva or pupa). Adult overwinterers were excluded due to the challenges of estimating phenological metrics for the initiation of the adult flight period in the spring, and migrants were excluded because individuals' geographical origins are unknown.

We intentionally chose a species-neutral, trait-based approach, as insect occurrence data are often insufficient for broad-scale species-level analyses. We identified overwinter stage (OWS) as our focal trait, given that the stage for overwinter diapause has been repeatedly shown to be a strong predictor of phenology, phenological sensitivity and abundance (Breed et al., 2013; Diamond et al., 2011, 2014; Karlsson, 2014). We applied this approach to the butterfly clade, which provides a crucial trophic link converting plant biomass to nutrient-rich prey, as well as important pollination services as adults.

Within the butterfly clade, the contributions to ecosystem function are relatively consistent across species, and are generally related to abundances. We therefore aggregated data across species by OWS to estimate phenology and abundance metrics (Larsen et al., 2022). Because our data aggregations preclude directly addressing phylogenetic autocorrelation and OWS is known to be phylogenetically clustered, we used multiple lines of evidence to carefully test the robustness of this approach. We assessed the phylogenetic breadth of our sampling within each OWS group; each stage included species from multiple families (two in egg overwinterers, five in larval overwinterers and four in pupal overwinterers, out of the five described families in the study region; details in Appendix S1). We also mapped overwintering stages of the species pool we included to the species phylogeny constructed by Earl et al. (2021), which included 1437 of the known butterfly species of North America (Appendix S1). This mapping demonstrates that our sampling has strong phylogenetic breadth across all diapause stages, and evidence for at least five independent originations of egg overwintering among the sampled taxa. To directly assess the influence of phylogeny on observed abundance patterns, we further conducted a separate reanalysis of published species-specific abundance trends (briefly summarized in the discussion and further detailed in Appendix S2). In sum, while our main analyses do not directly account for phylogenetic autocorrelation, our pooling by overwintering stage broadly covers multiple major clades across the full butterfly tree of life, and we found no evidence that our analysis was confounded by phylogenetic autocorrelations (Appendix S2).

2.2 | Butterfly data sources

All adult butterfly phenology and abundance metrics were derived from community science (aka citizen science) observations, which provide broad spatial coverage within the study domain. Incidental records were aggregated from three community science platforms: iNaturalist, eButterfly and the North American Butterfly Association (NABA) to estimate adult phenology metrics. Incidental data were obtained directly from eButterfly (Prudic et al., 2017) and the NABA 'Butterflies I've Seen' and 'Recent Sightings' programs (Taron & Ries, 2015), while iNaturalist butterfly observations were

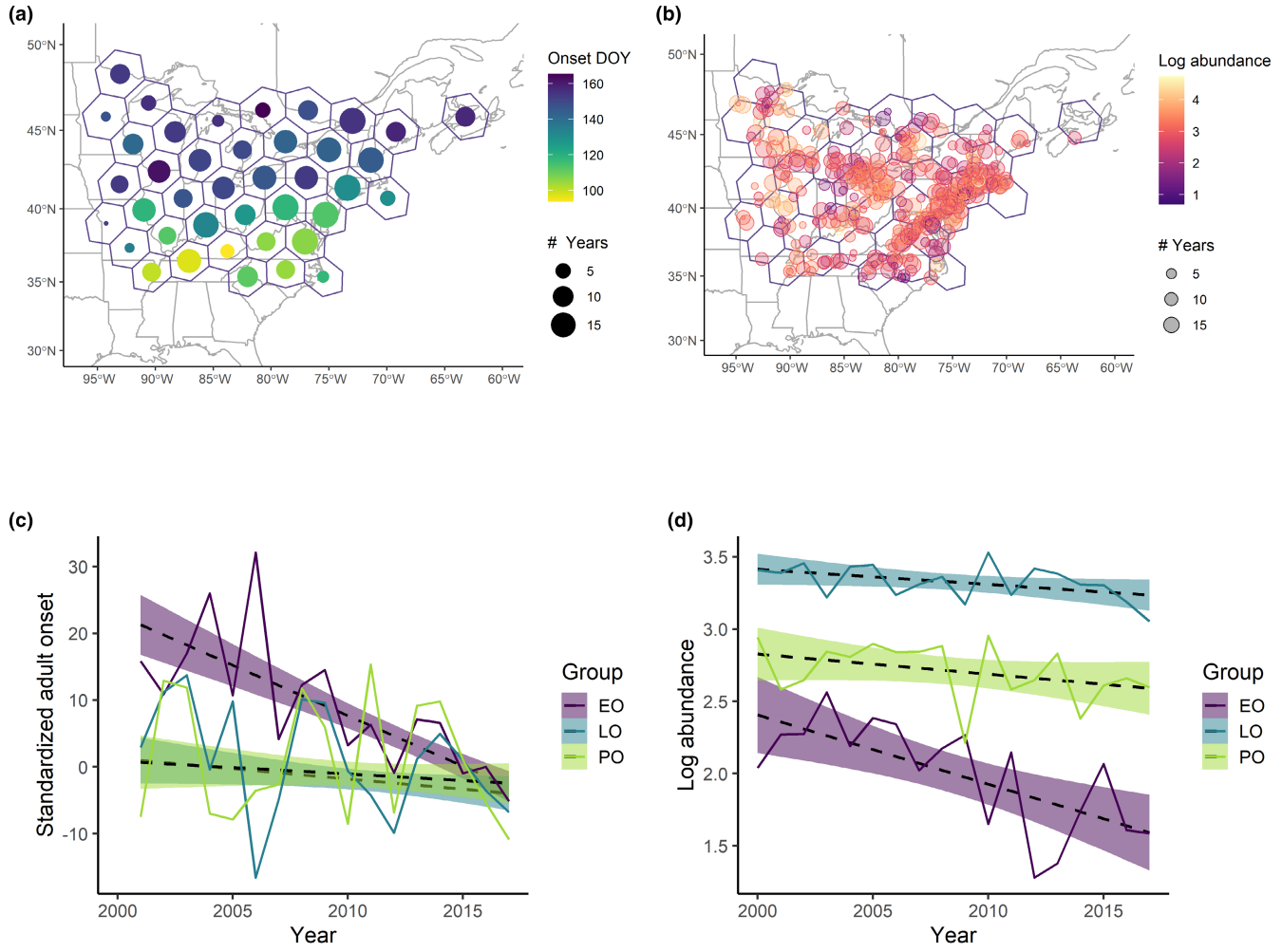

FIGURE 1 (a) Points centred in hex cells in study, coloured by the mean onset of adult flight period for larval overwinterers within this study and sized by number of years with phenology metrics for this group; (b) point locations of count data overlaid on hex cells in study, coloured by the mean log abundance of larval overwinterers (LO), sized with area proportional to number of survey years; (c) phenology dynamics across the study period: solid lines show the annual means of within-cell annual deviations of adult flight onset phenometrics by overwinter stage; (d) abundance dynamics across the study period: solid lines show annual mean survey abundances by overwinter stage (natural log scale). For (c) and (d), dashed lines & shaded areas show the overall temporal trends & 95% confidence intervals [in onset deviation & abundance metrics by group] as seen in the data, prior to analysis.

accessed via GBIF (GBIF.org, 2020, 2021). GBIF hosts research-grade iNaturalist records, meaning they are georeferenced, include photos, have a date, are identified to species by multiple users, and are not artificially reared (Seltzer, 2019). While iNaturalist observations are largely of adults, we did not want phenometrics to be biased by observations of other life stages, so we removed any observations labelled in iNaturalist as larvae by excluding all records in the Caterpillars of Eastern North America iNaturalist project. This project includes all lepidopteran observations annotated as larvae for our entire study area. We did not address potential egg and pupal observations, as research-grade records of these butterfly life stages are extremely rare. Incidental records obtained from the eButterfly and NABA 'Butterflies I've Seen' and 'Recent Sightings' programs were assumed to be of adults. We chose to use only incidental observations to generate phenometrics since these data integrate easily across platforms, produce robust phenology metrics (Belitz et al., 2020) and show similar patterns to structured survey data (Larsen et al., 2022).

For adult abundance estimates, we used count data from the NABA seasonal butterfly count program, a separate semi-structured survey program that tracks effort as well as observed abundances within survey sites (Taron & Ries, 2015). This program uses circular survey sites 15 miles in diameter, within which 1-day count surveys are conducted. For each survey, groups and individuals reported species' observed adult abundances as well as the number of participant party hours. We only included surveys conducted in June–August that reported at least 10 species (across all species groups) to limit seasonal variation in abundances and ensure sufficient survey effort. Each survey represented one site-year, and surveys were only included for sites with at least two site-years. At the time of analysis, incidental records used for phenological metrics were available through 2019, while count data used for abundance metrics were

only available through 2017. Because adult abundance and phenology are estimated from independent data sets, we are able to address the consequences of adult phenology for summer abundances and possible phenological mismatch.

2.3 | Environmental variables: Vegetation phenology and climate

Spring plant phenology was extracted from the yearly mid-greenup data product using the MODIS Land Cover Dynamics (MCD12Q2) data product Version 6 (Freidl et al., 2019) following (Youngflesh et al., 2021). The Land Cover Classification System from the Food and Agriculture Organization, provided in the MCD12Q1 v.6 data product and which uses the same spatial grid, was used to filter MCD12Q2 pixels by land cover type. Canopy greenup was estimated using pixels classified as forest (evergreen needleleaf forests, evergreen broadleaf forests, deciduous needleleaf forests, deciduous broadleaf forests, mixed broadleaf/needleleaf forests, mixed broadleaf evergreen/deciduous forests, open forests or sparse forests) or open canopy (dense herbaceous, sparse herbaceous, dense shrublands, shrubland/grassland mosaics or sparse shrublands) in the year 2017 as provided by the MCD12Q1 product. MCD12Q2 data for annual greenup phenology were extracted for these pixels, for all years with vegetation phenology quality scores of 'good' or 'best' in the MCD12Q2 product.

Summary greenup metrics were estimated for each year and hex cell in which at least 10,000 pixels met the above criteria, per Youngflesh et al. (2021). For each pixel, the MCD12Q2 mid-greenup product provided the estimated DOY at which the amplitude of the modelled Enhanced Vegetation Index reached half of its maximum. The DOY values for plant greenup phenology for a given hex cell, year and canopy type were calculated as the mean of the greenup DOY values for all relevant pixels. Because gree-nup timing between closed and open canopies often covary but differ, we calculated variables for mean forest canopy greenup DOY, and for open canopy lag, which we calculated as the differ-ence between the mean open canopy greenup DOY and the mean forest canopy greenup DOY.

Climate metrics were derived from daily temperature and precipitation data provided at 250 sq m resolution by the NOAA Physical Sciences Laboratory's Climate Prediction Center (NOAA PSL, 2021). We averaged daily precipitation and minimum and maximum temperatures within each cell to estimate seasonal climate variables for each cell-year combination. Seasonal precipitation was calculated as the sum of mean daily values within each cell and then standardized across years to *z*-scores. Winter conditions were calculated for the period between the fall equinox of the previous year (DOY_{i-1} 266) and the spring equinox (DOY_i 80). Spring and summer conditions were calculated between the spring equinox and summer solstice (DOY_i 80, 172) and the summer solstice and autumn equinox (DOY_i 172, 266), respectively, as these DOYs are relevant markers of seasons for the study area. Winter conditions were summarized with two temperature metrics: the number of days for which the maximum temperature was at or below 0°C (cold days), and the number of days for which the minimum temperature was above 0°C (warm days). Spring and summer temperatures were summarized as accumulated growing-degree days (GDD), a commonly used metric of energy available for growth in ectotherms. For each hex cell and day, a daily GDD value was estimated using a single-sine approximation of daily temperature curves and generic thermal limits of (10°C, 33°C) (Abarca et al., 2024; Cayton et al., 2015). Accumulated GDD values were calculated by summing the daily GDD values with a hex cell, year and season. While thermal limits vary across latitudes and taxa (Abarca et al. in press), any GDD values estimated using thresholds within known variation in insect phenology will be highly correlated with values using these generic limits (Appendix S1). All environmental variables were available for 2001–2019.

2.4 | Insect phenology metrics

Insect phenology metrics were calculated for species groups according to overwinter diapause stage (i.e. overwintering as eggs [EO], larvae [LO] or pupae [PO]). All incidental records were aggregated within years, hex cells and species groups defined by diapause stages prior to estimating phenology metrics. We set minimum data thresholds for estimating phenology from the aggregated incidental data of 15 occurrences on at least eight unique days. These thresholds were informed by previous work estimating phenology from both simulations and field-collected incidental data, and were selected to ensure robust phenological metrics while maximizing the spatiotemporal coverage of the analysis (Belitz et al., 2020; Larsen & Shirey, 2021). To correct for biases introduced by dates with extra survey effort, days with greater than the average number of observations given a particular year, cell and overwintering diapause stage were thinned to the average number of daily observations, following Li et al. (2021). From the remaining records, phenological metrics representing the adult flight period were estimated using a median of 46 occurrences (Figure 1a).

We extracted the 5th, 50th and 95th percentiles of occurrence day-of-year (DOY) values to estimate onset (5th), median (50th) and duration (difference between 95th and 5th) phenometrics, using the type 7 algorithm of the quantile() function in R, which returns continuous sample distributions of underlying distribution quantiles. These quantile metrics were selected to minimize bias in phenological metrics, per Belitz et al. (2020). Group-specific data density was calculated for each phenometric as the number of individual DOYs (summed across all observations) used in estimating that phenometric (Belitz et al., 2021). For each phenometric, confidence intervals were calculated by bias-corrected, accelerated bootstrapping via the R package Phenesse (Belitz et al., 2020), which were used to weight onset and duration phenometric estimates (see more below). Data visualizations were used to examine phenometrics for potential outliers, which were typically associated with lower data densities (Appendix S1).

Because all species groups pooled species of different voltinisms and seasonalities, all groups were expected to have their median flight time in summer; after data exploration, phenometrics were excluded for cell-year-group combinations where the median phenometric was outside of June–August (DOY 152–243; Figure S1.2; $n = 49$). Larval and pupal overwinterers (LO and PO, respectively) were well represented in the available phenology metrics ($n = 398$ and 353 cell years, respectively), while phenometrics for egg overwinterers (EO) were sparser ($n = 133$) (see also Figure S1.3). Onset and duration metrics were used in our analysis as key metrics of butterfly flight phenology. Duration was also used to examine the seasonal interpretation of single-survey abundance results.

2.5 | Annual deviation metrics

As expected across such a broad region, latitudinal trends in phenology are strong and significant (Figure 1a). To account for prevailing patterns in average conditions and phenology across space, and focus on interannual dynamics, we developed annual deviation metrics for phenology and environmental variables. Because phenology and environmental variables were available for more recent years than abundance data, we calculated baseline values using a 4-year period (2016–2019), which partially overlapped the study period (2001–2017). This maximized the spatial scope for which annual deviation metrics were calculable. A period of 4 years was chosen to provide a consistent baseline from which to capture interannual variation without sacrificing spatial coverage.

For each cell-group combination, annual deviation (AD) metrics were calculated as the difference between each phenometric and its baseline, such that positive values indicate later phenology (Figure 1c). Group-specific baseline phenology metrics were calculated only for cells with group-specific metrics in all baseline years ($n = 13$ cells for EO, $n = 37$ cells for LO and $n = 34$ cells for PO). Annual deviation metrics were also calculated for environmental variables (winter cold days, winter warm days, spring GDD, forest greenup DOY, open canopy lag, summer GDD) using the same approach. Annual deviations for spring GDD and forest greenup DOY were collinear and combined in a principal components analysis, resulting in PC1 (accounting for 78% of variance) and PC2 (22% of variance). PC1 represents 'warm and early' years (for which higher values indicate higher spring GDD and earlier forest greenup) for a given hex cell, and PC2 represents forest greenup phenology deviations from that expected based on hex cell and GDD (in which negative values indicate greenup earlier than expected and positive values indicate later than expected). PC1 and PC2 were then scaled to units of days of greenup shifts for easier interpretation of relative phenology shifts.

2.6 | Insect abundance metrics

As a proxy for contributions to ecosystem processes, abundance metrics were calculated for species groups according to diapause strategy (eggs, larvae, pupae) for 2001–2017 (Figure 1b). For each NABA seasonal survey, abundance totals for each species were divided by the reported number of party hours to correct for variable effort (Swengel & Swengel, 2015; Taron & Ries, 2015), and values above 100 'butterflies per party hour' were removed from analysis as outliers, which likely reflected non-typical population dynamics of a small portion of records and would have undue leverage on community abundance metrics (0.12% of all records; over half were the non-native European skipper *Thymelicus lineola*, representing 5% of *T. lineola* records; these extreme abundances comprised less than 2% of records for all other species). The remaining species values were aggregated by summing within species groups to estimate group abundance metrics for each survey (median 4 surveys per cell year, range 1–27), which were transformed on a natural log scale prior to analysis (Figure 1b). More species overwinter as larvae (LO) or pupae (PO) in the focal community, and these groups showed higher overall abundances compared to those that overwinter as eggs (EO, Figure 1d). All groups showed declines over time (Figure 1d), as has been shown in other analyses within the same region (Breed et al., 2013; Wepprich et al., 2019).

2.7 | Statistical analysis

We used weighted mixed effects linear models to test for drivers of interannual variation and trends in phenology and abundance metrics. For phenology, the annual deviations of phenology metrics were modelled using fixed effects for the overwinter diapause stage and its interactions with environmental covariates, year and group-specific data density (number of unique observation days); random intercepts were estimated for each hex cell. Model inputs were weighted by the inverse of the phenometric confidence interval size. The environmental covariates used for onset models comprised the annual deviations of environmental covariates for warm winter days and open canopy lag, as well as PC1 (a spectrum from cooler spring temperatures and later forest greenup to warmer spring temperatures and earlier forest greenup, in which positive values represent warmer & earlier spring metrics) and PC2 (a measure of GDD-plant leaf-out decoupling, in which positive values indicate later greenup than expected). Duration models included these variables as well as the annual deviations of summer GDD. To address the spatiotemporal dynamics of phenology, DOY phenology metrics were also modelled in parallel analyses using spatiotemporal environmental covariates (Appendix S3).

Abundance metrics were modelled using fixed effects for the overwinter diapause stage and its interactions with environmental covariates, adult butterfly phenology (adult onset and duration, see above), year and survey-specific corrections; random intercepts were estimated for survey sites nested within cells. For abundance, environmental covariates included PC1 and PC2 and within-cell annual deviations of cold winter days and open canopy lag. Survey-specific corrections included previous year abundance, survey day nested within survey month and the absolute

number of days between the survey and the group-specific phenological median.

All analyses were conducted in R (4.0.2) using tidyverse (R Core Team, 2021; Wickham et al., 2019) and lme4 (Bates et al., 2015). Model selection was performed using AIC. Marginal and conditional *R*-squared values were estimated using the package MuMIn (Barton, 2022). Variance inflation factors (VIFs) were reviewed to assess collinearity for final model terms without interactions and ensure VIFs < 5 using package car (Fox & Weisberg, 2019).

3 | RESULTS

3.1 | Phenology trends and drivers

Variation in adult onset phenology was strongly associated with climate for all groups (marginal $r^2 = 0.46$, conditional $r^2 = 0.71$; Table 1). The best model of annual deviations in adult onset included win-ter and spring precipitation as well as variables derived from spring temperatures and greenup (PC1, warm spring and early greenup, and PC2, greenup later than expected given climate). Winter and spring precipitation, as well as PC2, had different impacts according to the diapause stage (Figure 2). Higher PC1 was associated with earlier adult flight onset for all groups, shifting 0.31 ± 0.06 days for each day of greenup advance ($p < 0.001$). PC2 had an effect on adult onset for LO only, with adult onset shifting 0.82 ± 0.16 days later per day of later greenup ($p < 0.001$). We did not find evidence that PC2 influenced the interannual variation in onset for EO or PO. Higher winter precipitation was associated with delayed adult onset for both larval and pupal overwinterers. On the other hand, more spring precipitation was associated with earlier adult onset, but only for pupal overwinterers (Table 1). While accounting for environmental drivers, group-specific year effects were evident, with egg overwinterers trending earlier in recent years, and pupal overwinterers trending later (Figure 2). This best model also included fixed effects for data density and random intercepts by hex cell. As expected, earlier onset phenology estimates occurred with a higher data density (Table S1.4).

Variations in flight season duration were similarly associated with climate. Our model indicated that higher summer GDD, lower summer precipitation and additional winter warm days were all associated with longer flight seasons for all groups (Table S1.5). High PC1 (warm spring + early greenup) was associated with longer durations for egg (1.24 ± 0.44 days for each day of greenup advance) and pupal (0.47 ± 0.2 days) overwinterers, but not larval. Flight season duration for larval overwinterers was also associated with PC2, with flight periods shorter by 2.29 ± 0.32 days for every day of later than expected greenup. Higher spring precipitation was associated with longer durations for EO only, and for PO, shorter flight periods were associated with longer lags between forest and open canopy greenup. The best model for annual deviations in flight duration also included fixed effects for data density and year as well as random intercepts by hex

TABLE 1 Parameterization for variables of interest in the final onset phenology and abundance models.

	Overwintering group, mean estimate (SE)			
Variable	**ALL**	**EO**	**LO**	**PO**
Phenology: Onset variation				
PC1	−0.31 (0.06)**	—	—	—
PC2	—	−0.12 (0.40)	0.82 (0.16)**	−0.09 (0.18)
Winter precip	—	2.5 (6.5)	8.2 (3.4)*	17.9 (3.4)**
Winter warm days	−0.10 (0.05)*	—	—	—
Spring precip	—	7.0 (6.4)	3.8 (2.7)	−7.1 (3.3)*
Year	—	−1.13 (0.31)**	0.04 (0.17)	0.44 (0.17)*
Abundance: Log (butterflies per-survey hour)				
PC1	—	−0.022 (0.004)**	0.008 (0.002)**	0.005 (0.002)*
PC2	—	0.015 (0.010)	0.016 (0.004)**	−0.014 (0.005)*
Open canopy lag	—	0.045 (0.008)**	−0.002 (0.004)	−0.023 (0.004)**
Adult flight period duration	—	0.038 (0.010)**	−0.014 (0.005)*	−0.008 (0.006)
Year	—	−0.041 (0.009)**	−0.015 (0.004)**	0.006 (0.004)
Winter cold days	—	0.025 (0.003)**	−0.00094 (0.0015)	−0.00028 (0.0015)
Spring precip	—	0.49 (0.18)*	−0.03 (0.8)	−0.02 (0.09)
Summer GDD	0.06 (0.02)**			
Adult onset	−0.016 (0.008)*			

Note: All explanatory variables other than year were represented by interannual deviations from a within-cell baseline. For onset phenology deviations final model marginal $r^2 = 0.46$, conditional $r^2 = 0.71$ (with random cell intercepts; correction variables in Table S1.4). For abundance final model marginal $r^2 = 0.65$, conditional $r^2 = 0.67$ (with random intercepts for cell and CountID within cell; correction variables in Table S1.6).
*$p < 0.05$. **$p < 0.001$.

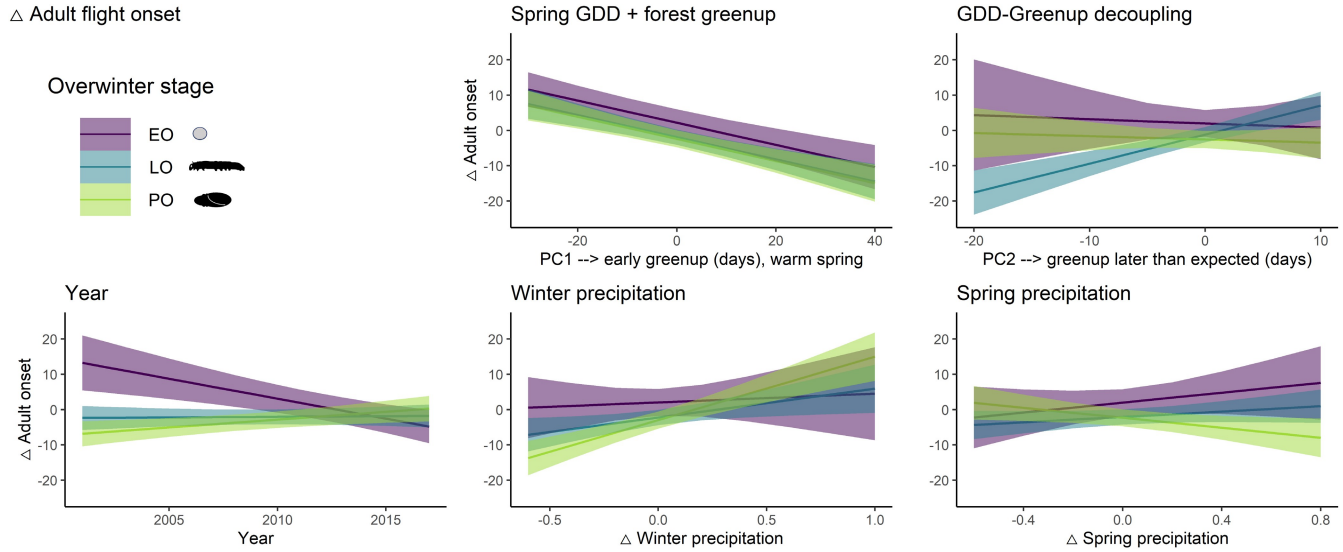

FIGURE 2 Model results for the onset phenology of resident butterfly groups defined by the overwinter stage. Along the top row, the middle panel shows the consistent response across trait groups to warmer springs and earlier greenup (higher PC1), and the right panel shows the strong response of larval overwinterers towards later adult onset when greenup is later than expected (higher PC2). In the bottom row, the left panel shows the strong shift over time towards earlier adult onset of egg overwinterers compared to larval and pupal overwinterers; the middle panel shows the variable sensitivity of different groups to winter precipitation; and the right panel shows earlier onset for PO and later onset for EO in years with more spring precipitation.

cell (marginal $r^2=0.62$, conditional $r^2=0.96$; Table S1.5). Across the 17 years of the study, and separate from environmental drivers, adult flight durations shortened for LO and PO, and lengthened for EO.

3.2 | Abundance trends and drivers

Group abundance dynamics and drivers were strongly conditioned by the overwinter diapause stage. The best model for abundance included group-specific effects for climate, plant greenup phenology, adult flight phenology and year (marginal $r^2=0.65$, conditional $r^2=0.67$, Table 1). This model also corrected for survey timing and site-specific effects (Table S1.6). Group-specific effects were supported for several metrics of climate and greenup: PC1, PC2, winter cold days, spring precipitation and open canopy greenup lags (Figure 3). In years with high PC1 (warm springs and early greenup; Figure 3), surveys detected lower abundances of EO (−0.023 ± 0.009) and higher abundances of LO (0.008 ± 0.004) and PO (0.005 ± 0.004). PC2 was not associated with variation in EO abundances, but high PC2 (later greenup relative to spring GDD) was associated with higher abundances for LO (0.016 ± 0.008) and lower abundances for PO (−0.014 ± 0.009; Figure 3). More egg overwinterers (0.045 ± 0.015) and fewer pupal overwinterers (−0.023 ± 0.009) were observed in years with later open canopy greenup relative to forest greenup. Survey abundances were also higher for only EO following winters with more frequent cold days (0.025 ± 0.005) and particularly in years with more spring precipitation (0.49 ± 0.34). The best model did not include a group-specific effect for summer GDD, but there was very strong evidence that higher summer GDD was associated with higher abundances across diapause stages.

Beyond the direct effects of climate and plant phenology, adult butterfly phenology metrics and survey abundances were also related. Later adult flight season onset was associated with lower survey abundances (−0.016 ± 0.014) across all overwinter stages. Further, only EO survey abundances were higher (0.0.038 ± 0.019) in years with longer estimated flight seasons, though longer flight seasons were associated with lower survey abundances for LO (−0.014 ± 0.01). Finally, after accounting for environmental conditions and phenology, we identified trends towards lower abundances in recent years for both EO (−0.01 ± 0.017) and LO (−0.015 ± 0.008). There was no evidence of a temporal trend in the abundance of PO after accounting for environment and survey factors.

4 | DISCUSSION

Our results demonstrate that aggregate butterfly phenology and abundance differ dramatically according to their overwinter diapause stage and their interaction with climate and plant phenology. Inherent in these results are indications of potential phenological mismatches, given that our modelling framework directly determined differentials between climate, plant phenology and butterfly phenology, all in relation to abundance. These mismatches may be in relation to hostplant resources, predators and parasitoids and/ or to climate itself. Below, we first address key phenology shifts, relative to climate and plant phenology, and how those manifest across overwintering stages, and then frame abundance declines in relation to these phenology findings and their potential ecosystem consequences.

A key question our phenology models addressed was how climate and plant phenology drivers impact adult flight onset. Across

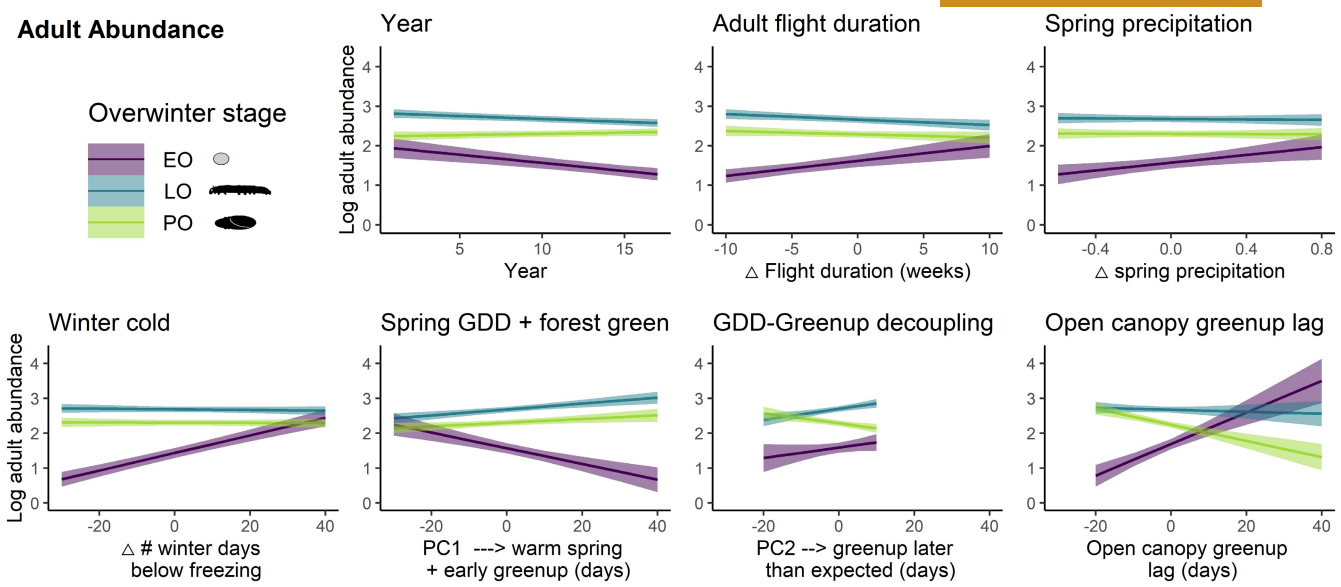

FIGURE 3 Panels demonstrating the model predictions of specific variables (year, adult flight period duration, spring precipitation, winter cold days, PC1, PC2 and open canopy greenup lag) for (log-scale) survey abundance of each group aggregated by overwinter diapause stage. Numeric model results are provided in Table 1.

groups, adult onset phenology was advanced in years with more winter days above freezing and years with warmer springs and earlier forest greenup, though the magnitude of advance for flight period onset was only a fraction of the greenup advance. Further, only larval overwinterers demonstrated delayed adult onset and shortened flight duration when forest greenup was not as early as expected for a given spring GDD. If greenup is a reliable proxy for hostplant phenology, the sensitivity of developmental phenology to food resource availability may be greatest for larval overwinterers, due to greater initial resource needs post-diapause. Greater winter precipitation was associated with later adult flight onset for larval overwinterers, but even more so for pupal overwinterers. Further, the adult phenology of pupal overwinterers was earlier in years with greater spring precipitation, indicating the complexity of phenological responses to seasonal timing (and likely the form) of precipitation. However, given that these precipitation metrics do not distinguish between rain and snow, more work is needed to understand these impacts. Overall, the timing of ecosystem service provision by these herbaceous insects is affected by both temperature and precipitation, in ways that are likely to impact relative synchrony with plant phenology, specifically greenup, and possible flowering timing as well.

We found a strong trend towards earlier adult onset of egg overwinterers across years after accounting for environmental drivers, exacerbating already-strong environmental-based phenological shifts. Earlier diapause termination and hatching, faster larval and pupal development and abbreviated larval development could each be contributing to earlier adult onset of egg overwinterers in recent years. For pupal overwinterers, a temporal trend towards later adult onset, opposite that seen in egg overwinters, dampened environment-related phenological advances. This trend may indicate shifts towards suboptimal winter temperatures not captured by our winter metrics, affecting diapause termination and post-diapause development (Lehmann et al., 2017; Toxopeus et al., 2023). Larval overwinterers are the only group who don't exhibit strong temporal shifts after accounting for environmental effects. These contrasting phenological responses across butterfly diapause strategies may reflect a combination of differential phenotypic plasticity, adaptive responses in the face of change or dissimilar environmental cues used to terminate diapause. Further work is needed to directly test these different, non-mutually exclusive underlying mechanisms.

Determining multi-trophic phenology and abundance relationships is essential for better understanding the consequences of global change for ecosystem processes (Iler et al., 2021). For developing Lepidoptera, life stages are differentially exposed to spring conditions and should face different mortality risks. Early larval stages are likely to be more vulnerable to both extreme climate events and plant phenology timing, particularly related to issues with establishment and feeding (Cornell & Hawkins, 1995; Peterson et al., 2009). This vulnerability may be especially acute for insects overwintering as eggs, where warmer winters could drive earlier diapause termination, with the double jeopardy of limited food and a higher risk of sublethal or lethal temperatures during early-season cold snaps. Insects overwintering as later-instar larvae may experience less thermal variability during post-diapause development, and can mitigate climatic variation through behavioural thermoregulation, while those overwintering as pupae are not directly tied to plant food resources (Lehmann et al., 2017; Nice & Fordyce, 2006; Nielsen & Papaj, 2015). These later stages are therefore expected to have less vulnerability to spring-time phenological mismatch with lower trophic levels. Below, we lay out the key abundance results per diapause stage with the goal of dissecting where we have the strongest evidence of trophic mismatches and disruption of ecosystem services, and whether key predictions by the overwintering stage are supported or not.

We found strong evidence of striking abundance declines in butterflies that overwinter as eggs, as well as potential indications of trophic mismatches. This group demonstrated lower abundances in years with fewer winter days below freezing, with warmer spring temperatures and earlier forest greenup, with less spring precipitation and with earlier open canopy greenup relative to forest phenology. Lower abundances driven by advancing plant phenology may be due to difficulties for early-instar larvae establishing and feeding on more mature leaves or shifts in relative phenology with parasitoids and predators (Van Nouhuys & Lei, 2004). Warmer springs could also cue earlier diapause termination and increase the risk of mortality from extreme weather events. Further, egg overwinterers were the only group with abundances sensitive to winter temperatures, as fewer cold winter days were also associated with lower summer abundances. Finally, egg overwinterers also showed sharp abundance declines over time, after accounting for the impacts of environmental drivers. In sum, egg overwinterers show strong sensitivity and vulnerability to shifts in climate and plant phenology. Thus, there is reason for concern for this group in particular, and the timing and magnitude of ecosystem services, given that current climate models project warming temperatures across much of North America, with the greatest warming in the north (IPCC, 2021). As the group with the latest adult emergence, the declining abundance and advancing phenology of this group may be restricting the availability of optimal food resources for higher trophic levels within certain temporal windows of the growing season, particularly if these patterns hold for across lepidopterans. Further, egg-overwintering butterflies were the only group to demonstrate higher survey abundances in conjunction with longer flight seasons. While larger single-day survey abundances and longer observed flight periods could jointly be indicative of larger population sizes, we would expect such a pattern to be consistent across all groups, which was not the case. The presence of this relationship for only egg overwinterers may indicate that variation in phenology timing among these insects mitigates group-wide vulnerabilities due to phenological mismatch.

For larval overwinterers, both earlier adult onset and higher adult abundances were associated with years with warmer spring temperatures and earlier greenup. However, when greenup was earlier than expected based on GDD (low PC2), adult onset was earlier, and survey abundances were lower. Given that adult onset phenology shifted with plant phenology (quantified in both PC1 and PC2), larval overwinterers may better match the spring phenological shifts of host–plants, though early spring activity may still increase vulnerabilities. More work is needed to understand how these abundance shifts impact ecosystem services provided by both larval and adult stages. Larval overwinterers also demonstrated lower abundances when flight duration is longer, which may seem counterintuitive; however, our abundance estimates were from single surveys, not an accumulation across the season (contrary to Michielini et al., 2021). Thus, lower survey abundances for larval overwinterers in years with longer durations could be related to individual variation in phenology (i.e. the same number of individuals spread out across a longer time). Across years, larval overwinterers showed no sign of additional phenology shifts, unlike egg overwinterers, and generally demonstrated modest per-survey declines in abundance.

Pupal overwinterers were expected to be most resistant to climate and plant phenology drivers in early spring since they are least tied to food resources. However, we found that abundances of pupal overwinterers were slightly higher in years with warmer spring temperatures and earlier forest greenup, but lower when forest greenup was later than expected based on GDD, and particularly when open canopy greenup was later relative to forest phenology. Interestingly, the adult phenology of pupal overwinterers were strongly affected by seasonal precipitation, in ways that merit further examination. Given that onset phenology for pupal overwinterers appears more linked to climate than plant phenology, we hypothesize that abundance dynamics may be related to increased top-down predation pressure associated with eclosion prior to leaf-out.

Using the same underlying count data and a different set of traits, Crossley et al. (2021) examined species abundance trends and found evidence for climate but not traits driving heterogeneous trends. The traits (colour, size, larval hairs and host plant breadth) selected by Crossley et al. (2021) targeted potential trophic interactions but did not incorporate different phenological sensitivities. Though we were not interested in species-specific trends, we conducted a reanalysis of the abundance trends presented by Crossley et al. (2021), which incorporated the overwinter diapause stage into a phylogenetic mixed effects linear model (Appendix S2). The diapause stage remains a key factor explaining abundance trends after directly accounting for phylogeny in our reanalysis (Appendix S2). Using these multiple lines of evidence, we show that the diapause stage has profound consequences for phenology and abundance dynamics in temperate regions and in the context of climate change, demonstrating the importance of life history traits with direct ties to phenology and future abundance trends. These findings are consistent with findings that the overwintering stage plays an important role for flight timing shifts for odonates (Patten & Benson, 2023) and bees (Stemkovski et al., 2020), as well as abundance dynamics in bees (Pardee et al., 2022).

While our focus is the Eastern USA, these results may translate to other areas, as suggested by our Crossley et al. (2021) reanalysis. This may be particularly useful in the Southwest, where stronger declines are predicted (Crossley et al., 2021; Forister et al., 2021). In an analysis of western US montane butterflies, Nice et al. (2014) examined the role of the overwinter diapause stage in relating observation frequency to climate, and also found that, on average, egg-diapausing butterflies were affected more negatively by warmer minimum and maximum temperatures in winter and spring. This provides further evidence that egg-overwintering butterflies are at risk of climate warming. While this group demonstrated lower abundances throughout the study period, more work is needed to understand the historical abundances of this group and their longer-term trajectory. We encourage extensions to the framework we have developed, considering other environmental factors and taxonomic groups contributing to different ecosystem processes. Additionally,

species or trait group-specific developmental models may better elucidate the ecophysiological responses across life stages in relation to population change. We expect that other traits, such as voltinism, also play an important role in determining the interactions between phenology and abundance (Macgregor et al., 2019; Michielini et al., 2021).

The abundance declines observed here align with other reports of declines of both insects and higher trophic levels, and indicate the potential for broad ecosystem impacts. The Lepidopteran larval stage particularly comprises a critical link transferring energy up trophic levels, and have been implicated in declines of bird populations (Grames et al., 2023; Perrins, 1991; Tallamy & Shriver, 2021). Given our focus on adult—rather than larval—abundance and phenology, our framework cannot directly elucidate the strength of these top-down and bottom-up trophic interactions, nor fully separate the effects of seasonal climate variability versus phenology shifts. Still, adult abundance declines along with declines at higher trophic levels, and clear linkages to larval thermal biology strongly suggest that larval abundance is also declining, with particular risk for egg overwinterers. Expanding insect monitoring efforts for different life stages is critical for better understanding the impacts of macrophenological shifts across trophic levels. Broad-scale, standardized monitoring systems (e.g. Caterpillars Count!, Hurlbert et al., 2019) or frass monitoring (Zandt, 1994) can provide the needed data basis for more direct comparisons between larval seasonal abundances, plant leaf-out and top-down predation timing (e.g. bird nestling provisioning, Youngflesh et al., 2021).

The key importance of this study is that it showcases how key traits related to phenology responses critically impact fitness under environmental change, and the potential consequences for spatiotemporal changes in ecosystem services. In particular, our work shows that the overwinter diapause strategy has profound consequences for phenology and abundance dynamics related to climate in this clade of insects. Because the diapause strategy is a simple trait that is often known for species and consistent across temperate ranges, it may serve as a key proxy for the fate of larval and adult insect abundance exposed to environmental change. Our work clearly demonstrates that in our study region, egg-overwintering butterflies are at highest risk under future climate change, likely due to both trophic-level mismatches and vulnerability to winter and spring climate variability. Further, our framework provides predictions to be tested in other holometabolous insect groups. Understanding how life history traits mediate insect phenology and abundance will help forecast and potentially mitigate climate change impacts on biodiversity and ecosystem function.

AUTHOR CONTRIBUTIONS

Elise A. Larsen, Michael W. Belitz, Grace J. Di Cecco, Allen H. Hurlbert, Leslie Ries and Robert P. Guralnick conceived the ideas and designed methodology; Allen H. Hurlbert, Leslie Ries and Robert P. Guralnick acquired funding for this work. Jeffrey Glassberg contributed substantial data; Elise A. Larsen and Michael W. Belitz curated and analysed the data. All authors were actively involved in decision making from analysis to manuscript. Elise A. Larsen led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

All R code for this work and associated files are available in a github repository (https://github.com/phenomismatch/bfly_spat.temp) and archived on Zenodo (https://doi.org/10.5281/zenodo.10661806). Github release 2.0 corresponds to the code and files associated with the final manuscript.

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REFERENCES

Abarca, M., & Lill, J. T. (2015). Warming affects hatching time and early season survival of eastern tent caterpillars. *Oecologia*, *179*(3), 901–912. https://doi.org/10.1007/s00442-015-3371-x

Abarca, M., Parker, A. L., Larsen, E. A., Umbanhowar, J., Earl, C., Guralnick, R. P., Kingsolver, J. G., & Ries, L. (2024). How development and survival combine to determine the thermal sensitivity of insects. *PLoS ONE*, *19*(1), e0291393. https://doi.org/10.1371/journal.pone.0291393

Barton, K. (2022). *MuMIn: Multi-model inference*. R package version 1.46.0. https://CRAN.R-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Belitz, M., Barve, V., Doby, J., Hantak, M., Larsen, E., Li, D., Oswald, J., Sewnath, N., Walters, M., Barve, N., Earl, K., Gardner, N., Guralnick, R., & Stucky, B. (2021). Climate drivers of adult insect activity are conditioned by life history traits. *Ecology Letters*, *24*(12), 2687–2699. https://doi.org/10.1111/ele.13889

Belitz, M. W., Larsen, E. A., Ries, L., & Guralnick, R. P. (2020). The accuracy of phenology estimators for use with sparsely sampled presence-only observations. *Methods in Ecology and Evolution*, *11*, 1273–1285. https://doi.org/10.1111/2041-210X.13448

Breed, G. A., Stichter, S., & Crone, E. E. (2013). Climate-driven changes in northeastern US butterfly communities. Nature. *Climate Change*, *3*(2), 142–145. https://doi.org/10.1038/nclimate1663

Buckley, L. B., Arakaki, A. J., Cannistra, A. F., Kharouba, H. M., & Kingsolver, J. G. (2017). Insect development, thermal plasticity and fitness implications in changing, seasonal environments. *Integrative and Comparative Biology*, *57*(5), 988–998. https://doi.org/10.1093/icb/icx032

Cardoso, P., Barton, P. S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C. S., Gaigher, R., Habel, J. C., Hallmann, C. A., Hill, M. J., Hochkirch, A., Kwak, M. L., Mammola, S., Noriega, J. A., Orfinger, A. B., Pedraza, F., Pryke, J. S., Roque, F. O., … Samways, M. J. (2020). Scientists' warning to humanity on insect extinctions. *Biological Conservation*, *242*, 108426.

Cardoso, P., Erwin, T. L., Borges, P. A. V., & New, T. R. (2011). The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation*, *144*(11), 2647–2655. https://doi.org/10.1016/j.biocon.2011.07.024

Cayton, H. L., Haddad, N. M., Gross, K., Diamond, S. E., & Ries, L. (2015). Do growing degree days predict phenology across butterfly species? *Ecology*, *96*(6), 1473–1479. https://doi.org/10.1890/15-0131.1

Cornell, H. V., & Hawkins, B. A. (1995). Survival patterns and mortality sources of herbivorous insects: Some demographic trends. *The American Naturalist*, *145*(4), 563–593. https://doi.org/10.1086/285756

Costello, M. J., Wilson, S., & Houlding, B. (2012). Predicting total global species richness using rates of species description and estimates of taxonomic effort. *Systematic Biology*, *61*(5), 871. https://doi.org/10.1093/sysbio/syr080

Crossley, M. S., Smith, O. M., Berry, L. L., Phillips-Cosio, R., Glassberg, J., Holman, K. M., Holmquest, J. G., Meier, A. R., Varriano, S. A., McClung, M. R., Moran, M. D., & Snyder, W. E. (2021). Recent climate change is creating hotspots of butterfly increase and decline across North America. *Global Change Biology*, *27*(12), 2702–2714. https://doi.org/10.1111/gcb.15582

Di Cecco, G., Barve, V., Belitz, M. W., Stucky, B. J., Guralnick, R. P., & Hurlbert, A. H. (2021). Observing the observers: How participants contribute data to iNaturalist and implications for biodiversity science. *BioScience*, *71*(11), 1179–1188. https://doi.org/10.1093/biosci/biab093

Diamond, S. E., Cayton, H., Wepprich, T., Jenkins, C. N., Dunn, R. R., Haddad, N. M., & Ries, L. (2014). Unexpected phenological responses of butterflies to the interaction of urbanization and geographic temperature. *Ecology*, *95*(9), 2613–2621. https://doi.org/10.1890/13-1848.1

Diamond, S. E., Frame, A. M., Martin, R. A., & Buckley, L. B. (2011). Species' traits predict phenological responses to climate change in butterflies. *Ecology*, *92*(5), 1005–1012. https://doi.org/10.1890/i0012-9658-92-5-1005

Earl, C., Belitz, M. W., Laffan, S. W., Barve, V., Barve, N., Soltis, D. E., Allen, J. M., Soltis, P. S., Mishler, B. D., Kawahara, A. Y., & Guralnick, R. (2021). Spatial phylogenetics of butterflies in relation to environmental drivers and angiosperm diversity across North America. *Iscience*, *24*(4), 102239.

Eskildsen, A., Carvalheiro, L. G., Kissling, W. D., Biesmeijer, J. C., Schweiger, O., & Høye, T. T. (2015). Ecological specialization matters: Long-term trends in butterfly species richness and assemblage composition depend on multiple functional traits. *Diversity and Distributions*, *21*(7), 792–802. https://doi.org/10.1111/ddi.12340

Forister, M. L., Halsch, C. A., Nice, C. C., Fordyce, J. A., Dilts, T. E., Oliver, J. C., Prudic, K. L., Shapiro, A. M., Wilson, J. K., & Glassberg, J. (2021). Fewer butterflies seen by community scientists across the warming and drying landscapes of the American west. *Science*, *371*(6533), 1042–1045.

Fox, J., & Weisberg, S. (2019). *An {R} companion to applied regression* (3rd ed.). Sage. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Freidl, M., Gray, J., & Sulla-Menashe, D. (2019). MCD12Q2 MODIS/Terra+aqua land cover dynamics yearly L3 global 500m SIN grid V006 [data set]. *NASA EOSDIS Land Processes DAAC*, https://doi.org/10.5067/MODIS/MCD12Q2.006

GBIF.org. (2020). *GBIF occurrence download (2020-10-27)*. https://doi.org/10.15468/dl.63x8zw

GBIF.org. (2021). *GBIF occurrence download (2021-09-22)*. https://doi.org/10.15468/dl.vm5x8p

Grames, E., Montgomery, G., Haddaway, N., Dicks, L., Elphick, C., Matson, T., Nakagawa, S., Saunders, M., Tingley, M., White, T., & Woodcock, P. (2019). *Trends in global insect abundance and biodiversity: A community-driven systematic map protocol*. Open Science Framework.

Grames, E. M., Montgomery, G. A., Youngflesh, C., Tingley, M. W., & Elphick, C. S. (2023). The effect of insect food availability on songbird reproductive success and chick body condition: Evidence from a systematic review and meta-analysis. *Ecology Letters*, *26*, 658–673. https://doi.org/10.1111/ele.14178

Groombridge, B., & Jenkins, M. (2002). *World atlas of biodiversity: Earth's living resources in the 21st century*. University of California Press.

Hällfors, M. H., Pöyry, J., Heliölä, J., Kohonen, I., Kuussaari, M., Leinonen, R., Schmucki, R., Sihvonen, P., & Saastamoinen, M. (2021). Combining range and phenology shifts offers a winning strategy for boreal Lepidoptera. *Ecology Letters*, *1–18*, 1619–1632. https://doi.org/10.1111/ele.13774

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., & De Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE*, *12*(10), e0185809. https://doi.org/10.1371/journal.pone.0185809

Hallmann, C. A., Zeegers, T., van Klink, R., Vermeulen, R., van Wielink, P., Spijkers, H., van Deijk, J., van Steenis, W., & Jongejans, E. (2020). Declining abundance of beetles, moths and caddisflies in The Netherlands. *Insect Conservation and Diversity*, *13*(2), 127–139. https://doi.org/10.1111/icad.12377

Halsch, C. A., Shapiro, A. M., Fordyce, J. A., Nice, C. C., Thorne, J. H., Waetjen, D. P., & Forister, M. L. (2021). Insects and recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(2), e2002543117. https://doi.org/10.1073/pnas.2002543117

Harvey, J. A., Tougeron, K., Gols, R., Heinen, R., Abarca, M., Abram, P. K., Basset, Y., Berg, M., Boggs, C., Brodeur, J., Cardoso, P., de Boer, J. G., De Snoo, G. R., Deacon, C., Dell, J. E., Desneux, N., Dillon, M. E., Duffy, G. A., Dyer, L. A., … Chown, S. L. (2023). Scientists' warning on climate change and insects. *Ecological Monographs*, *93*(1), e1553.

Høye, T. T., Loboda, S., Koltz, A. M., Gillespie, M. A. K., Bowden, J. J., & Schmidt, N. M. (2021). Nonlinear trends in abundance and diversity and complex responses to climate change in Arctic arthropods. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(2), e2002557117. https://doi.org/10.1073/PNAS.2002557117

Hurlbert, A., Hayes, T., McKinnon, T., & Goforth, C. (2019). Caterpillars count! A citizen science project for monitoring foliage arthropod abundance and phenology. *Citizen Science: Theory and Practice*, *4*(1). https://doi.org/10.5334/cstp.148

Iler, A. M., Caradonna, P. J., Forrest, J. R. K., & Post, E. (2021). Demographic consequences of phenological shifts in response to climate change. *Annual Review of Ecology, Evolution, and Systematics*, *52*, 221–245. https://doi.org/10.1146/annurev-ecolsys-011921-032939

IPCC. (2021). *Climate change 2021: The physical science basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R.

Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (Eds.)]. Cambridge University Press. https://doi.org/10.1017/9781009157896

Ju, R. T., Gao, L., Wei, S. J., & Li, B. (2017). Spring warming increases the abundance of an invasive specialist insect: Links to phenology and life history. *Scientific Reports*, *7*(1), 14805. https://doi.org/10.1038/s41598-017-14989-3

Karlsson, B. (2014). Extended season for northern butterflies. *International Journal of Biometeorology*, *58*(5), 691–701. https://doi.org/10.1007/s00484-013-0649-8

Kharouba, H. M., Paquette, S. R., Kerr, J. T., & Vellend, M. (2014). Predicting the sensitivity of butterfly phenology to temperature over the past century. *Global Change Biology*, *20*(2), 504–514. https://doi.org/10.1111/gcb.12429

Kharouba, H. M., Vellend, M., Sarfraz, R. M., & Myers, J. H. (2015). The effects of experimental warming on the timing of a plant-insect herbivore interaction. *Journal of Animal Ecology*, *84*(3), 785–796. https://doi.org/10.1111/1365-2656.12328

Kingsolver, J. G., & Buckley, L. B. (2020). Ontogenetic variation in thermal sensitivity shapes insect ecological responses to climate change. *Current Opinion in Insect Science*, *41*, 17–24. https://doi.org/10.1016/j.cois.2020.05.005

Larsen, E. A., Belitz, M. W., Guralnick, R. P., & Ries, L. (2022). Consistent trait-temperature interactions drive butterfly flight phenology in both incidental and survey data. *Scientific Reports*, *12*, 13370. https://doi.org/10.1038/s41598-022-16104-7

Larsen, E. A., & Shirey, V. (2021). Method matters: Pitfalls in analysing phenology from occurrence records. *Ecology Letters*, *24*(6), 1287–1289. https://doi.org/10.1111/ele.13731

Lehmann, P., Van Der Bijl, W., Nylin, S., Wheat, C. W., & Gotthard, K. (2017). Timing of diapause termination in relation to variation in winter climate. *Physiological Entomology*, *42*(3), 232–238. https://doi.org/10.1111/phen.12188

Li, D., Barve, N., Brenskelle, L., Earl, K., Barve, V., Belitz, M. W., Doby, J., Hantak, M. M., Oswald, J. A., Stucky, B. J., Walters, M., & Guralnick, R. P. (2021). Climate, urbanization, and species traits interactively drive flowering duration. *Global Change Biology*, *27*(4), 892–903. https://doi.org/10.1111/gcb.15461

Macgregor, C. J., Thomas, C. D., Roy, D. B., Beaumont, M. A., Bell, J. R., Brereton, T., Bridle, J. R., Dytham, C., Fox, R., Gotthard, K., Hoffmann, A. A., Martin, G., Middlebrook, I., Nylin, S., Platts, P. J., Rasteiro, R., Saccheri, I. J., Villoutreix, R., Wheat, C. W., & Hill, J. K. (2019). Climate-induced phenology shifts linked to range expansions in species with multiple reproductive cycles per year. *Nature Communications*, *10*(1). https://doi.org/10.1038/s41467-019-12479-w

McDermott Long, O., Warren, R., Price, J., Brereton, T. M., Botham, M. S., & Franco, A. M. (2017). Sensitivity of UK butterflies to local climatic extremes: Which life stages are most at risk? *Journal of Animal Ecology*, *86*(1), 108–116.

Michielini, J. P., Dopman, E. B., & Crone, E. E. (2021). Changes in flight period predict trends in abundance of Massachusetts butterflies. *Ecology Letters*, *24*(2), 249–257. https://doi.org/10.1111/ele.13637

Miller-Rushing, A. J., Høye, T. T., Inouye, D. W., & Post, E. (2010). The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *365*, 3177–3186. https://doi.org/10.1098/rstb.2010.0148

Nice, C. C., & Fordyce, J. A. (2006). How caterpillars avoid overheating: Behavioral and phenotypic plasticity of pipevine swallowtail larvae. *Oecologia*, *146*(4), 541–548. https://doi.org/10.1007/s00442-005-0229-7

Nice, C. C., Forister, M. L., Gompert, Z., Fordyce, J. A., & Shapiro, A. M. (2014). A hierarchical perspective on the diversity of butterfly species' responses to weather in the Sierra Nevada Mountains. *Ecology*, *95*(8), 2155–2168.

Nielsen, M. E., & Papaj, D. R. (2015). Effects of developmental change in body size on ectotherm body temperature and behavioral thermoregulation: Caterpillars in a heat-stressed environment. *Oecologia*, *177*(1), 171–179. https://doi.org/10.1007/s00442-014-3123-3

NOAA PSL. (2021). *CPC Global Temperature data*. NOAA PSL. https://psl.noaa.gov/data/gridded/data.cpc.globaltemp.html%0A

Noriega, J. A., Hortal, J., Azcárate, F. M., Berg, M. P., Bonada, N., Briones, M. J. I., Del Toro, I., Goulson, D., Ibanez, S., Landis, D. A., Moretti, M., Potts, S. G., Slade, E. M., Stout, J. C., Ulyshen, M. D., Wackers, F. L., Woodcock, B. A., & Santos, A. M. C. (2018). Research trends in ecosystem services provided by insects. *Basic and Applied Ecology*, *26*, 8–23.

Pardee, G. L., Griffin, S. R., Stemkovski, M., Harrison, T., Portman, Z. M., Kazenel, M. R., Lynn, J. S., Inouye, D. W., & Irwin, R. E. (2022). Life-history traits predict responses of wild bees to climate variation. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1973), 20212697.

Patten, M. A., & Benson, B. R. (2023). A broader flight season for Norway's Odonata across a century and a half. *Oikos*, *2023*, e09882.

Perrins, C. M. (1991). Tits and their caterpillar food supply. *Ibis*, *133*, 49–54.

Peterson, R. K. D., Davis, R. S., Higley, L. G., & Fernandes, O. A. (2009). Mortality risk in insects. *Environmental Entomology*, *38*(1), 2–10. https://doi.org/10.1603/022.038.0102

Prudic, K. L., McFarland, K. P., Oliver, J. C., Hutchinson, R. A., Long, E. C., Kerr, J. T., & Larrivée, M. (2017). eButterfly: Leveraging massive online citizen science for butterfly conservation. *Insects*, *8*(2). https://doi.org/10.3390/insects8020053

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Schwartzberg, E. G., Jamieson, M. A., Raffa, K. F., Reich, P. B., Montgomery, R. A., & Lindroth, R. L. (2014). Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees. *Oecologia*, *175*(3), 1041–1049. https://doi.org/10.1007/s00442-014-2960-4

Seltzer, C. (2019). Making Biodiversity Data Social, Shareable, and Scalable: Reflections on iNaturalist & citizen science. *Biodiversity Information Science and Standards*, *3*, e46670. https://doi.org/10.3897/biss.3.46670

Singer, M. C., & Parmesan, C. (2010). Phenological asynchrony between herbivorous insects and their hosts: Signal of climate change or pre-existing adaptive strategy? *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *365*(1555), 3161–3176. https://doi.org/10.1098/rstb.2010.0144

Stemkovski, M., Pearse, W. D., Griffin, S. R., Pardee, G. L., Gibbs, J., Griswold, T., Neff, J. L., Oram, R., Rightmyer, M. G., Sheffield, C. S., & Wright, K. (2020). Bee phenology is predicted by climatic variation and functional traits. *Ecology Letters*, *23*(11), 1589–1598.

Stewart, J. E., Illán, J. G., Richards, S. A., Gutiérrez, D., & Wilson, R. J. (2020). Linking inter-annual variation in environment, phenology, and abundance for a montane butterfly community. *Ecology*, *101*(1), e02906. https://doi.org/10.1002/ecy.2906

Swengel, A. B., & Swengel, S. R. (2015). Grass-skipper (Hesperiinae) trends in midwestern USA grasslands during 1988–2013. *Journal of Insect Conservation*, *19*(2), 279–292. https://doi.org/10.1007/s10841-015-9759-4

Tallamy, D. W., & Shriver, W. G. (2021). Are declines in insects and insectivorous birds related? *The Condor*, *123*(1), duaa059. https://doi.org/10.1093/ornithapp/duaa059

Taron, D., & Ries, L. (2015). Butterfly monitoring for conservation. In *Butterfly conservation in North America* (pp. 35–57). Springer Netherlands. https://doi.org/10.1007/978-94-017-9852-5_3

Toxopeus, J., Dowle, E. J., Andaloori, L., & Ragland, G. J. (2023). Variation in thermal sensitivity of diapause development among individuals

and over time drives life history timing patterns in an insect pest. *BioRxiv preprint*, https://doi.org/10.1101/2023.05.31.543112v1.full.pdf

Unger, S., Rollins, M., Tietz, A., & Dumais, H. (2020). iNaturalist as an engaging tool for identifying organisms in outdoor activities. *Journal of Biological Education*, *55*, 537–547. https://doi.org/10.1080/00219266.2020.1739114

van Klink, R., Bowler, D. E., Comay, O., Driessen, M. M., Ernest, S. K. M., Gentile, A., Gilbert, F., Gongalsky, K. B., Owen, J., Pe'er, G., Pe'er, I., Resh, V. H., Rochlin, I., Schuch, S., Swengel, A. B., Swengel, S. R., Valone, T. J., Vermeulen, R., Wepprich, T., … Chase, J. M. (2021). InsectChange: A global database of temporal changes in insect and arachnid assemblages. *Ecology*, *102*(6), e03354. https://doi.org/10.1002/ecy.3354

Van Nouhuys, S., & Lei, G. (2004). Parasitoid-host metapopulation dynamics: The causes and consequences of phenological asynchrony. *Journal of Animal Ecology*, *73*, 526–535.

Visser, M. E., & Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology & Evolution*, *3*(6), 879–885. https://doi.org/10.1038/s41559-019-0880-8

Wagner, D. L. (2020). Insect declines in the anthropocene. *Annual Review of Entomology*, *65*, 457–480. https://doi.org/10.1146/annurev-ento-011019-025151

Warren, M. S., Maes, D., van Swaay, C. A. M., Goffart, P., van Dyck, H., Bourn, N. A. D., Wynhoff, I., Hoare, D., & Ellis, S. (2021). The decline of butterflies in Europe: Problems, significance, and possible solutions. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(2), e2002551117. https://doi.org/10.1073/PNAS.2002551117

Wepprich, T., Adrion, J. R., Ries, L., Wiedmann, J., & Haddad, N. M. (2019). Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. *PLoS ONE*, *14*(7), e0216270. https://doi.org/10.1371/journal.pone.0216270

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D. A., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., … Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, *4*(43), 1686. https://doi.org/10.21105/joss.01686

Winfree, R., Fox, J. W., Williams, N. M., Reilly, J. R., & Cariveau, D. P. (2015). Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters*, *18*(7), 626–635.

Youngflesh, C., Socolar, J., Amaral, B. R., Arab, A., Guralnick, R. P., Hurlbert, A. H., LaFrance, R., Mayor, S. J., Miller, D. A. W., & Tingley, M. W. (2021). Migratory strategy drives species-level variation in bird sensitivity to vegetation green-up. *Nature Ecology & Evolution*, *5*, 987–994. https://doi.org/10.1038/s41559-021-01442-y

Zandt, H. S. (1994). A comparison of three sampling techniques to estimate the population size of caterpillars in trees. *Oecologia*, *97*, 399–406.

Zografou, K., Swartz, M. T., Adamidis, G. C., Tilden, V. P., McKinney, E. N., & Sewall, B. J. (2021). Species traits affect phenological responses to climate change in a butterfly community. *Scientific Reports*, *11*(1), 3283. https://doi.org/10.1038/s41598-021-82723-1

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Methodological details & complete model parameterization tables.

Appendix S2: Phylogenetic considerations.

Appendix S3: Spatiotemporal phenology models and results.

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